

OBSERVATIONS ON THE POLLINATION OF *DARWINIA FASCICULARIS* Rudge. [N.O. MYRTACEÆ].

BY AGNES A. BREWSTER.

(Plate lix.)

The late Mr. E. Haviland, in a paper published in the Proceedings of this Society, for 1884, Vol. ix., p. 67, dealt with the general structure, and the life-history of this plant; and my paper is intended to add some additional notes to his observations. The low shrubs flourish in sandstone-country, in exposed, sunny situations. The narrow, crowded leaves are well fitted for such conditions, for a cross-section of the leaf examined under the microscope shows that it has a thick layer of cuticle, which gives the stomates a sunken position. The palisade-tissue extends all round the leaf, and thus, with the aid of the cuticle, too rapid transpiration is prevented. There are two vascular strands in the centre of the leaf, embedded in colourless parenchyma.

Mr. Haviland described the flower-clusters, and the general structure of the flower. In the red clusters, the corollas of the flowers are white, except the lobes at the apex, which are red. There are ten stamens, with globular anthers, which dehisce by two pores. These alternate with ten staminodes.

I have noted, on microscopic examination of the corolla, that there are oil-glands dotted over the free lobes; and it is probably the evaporation of the volatile oils in these glands which gives the strong, peculiar perfume given out by the flowers in the sunshine. On crushing the foliage-leaves in the hand, there is a strong odour of rather oily eau-de-cologne.

Mr. Haviland says that, of a hundred of its flowers, ninety-five never open. I have noticed that every flower opens in the early stage of the flower, some remaining open for a longer period than others, but all the flowers close again in the later and longer stage

of their existence. As they do so, the lobes of the corolla fit round the lower part of the style, and may give some measure of support to this upstanding part of the flower.

The stamens are protandrous, ripening before the style begins to elongate, and just before the flower opens. They are in two whorls, each of the upper ones being placed in the middle of the corolla-lobes, the lower stamens occurring each at the junction of two of the lobes. The anthers are bent forward towards the centre of the tube; the benefit of this arrangement of the stamens will be pointed out later. If young anthers are placed on the micro-slide and mounted in water, and the cover-slip gently pressed, the pollen-sacs, four, may be plainly seen; in more mature anthers, there are only two loculi of the normal anther. The fibrous layer is beautifully shown, as is also the tapetal layer, which is disappearing.

Mr. Bentham (Fl. Austr., iii., 6), from the examination of herbarium-specimens, includes among the generic characters of *Darwinia*: "Style exerted, usually long, and more or less bearded towards the end." By the late Mr. E. Haviland, the bearded portion was thus described: "Immediately below the stigma is a ring of stiff hair-like glands, which secrete an adhesive fluid copiously"; and he suggested that these hairs secreted nectar, which was seen as a globule round the tuft of hairs, and which was carried up by the elongating style. I had found, on examining many buds, that these hairs extended across the flower so as to reach the anthers; and that just before the flower opens, the anthers give out a viscous mass in which the pollen-grains are embedded; and that it is this mass which adheres to the substigmatic tuft of hairs which extends between the two whorls of anthers, and is carried up by the elongating style. By this means, the pollen is placed in a very conspicuous position; and this fact, together with the colour of the flower-clusters, suggested bird-visitors, as the agents which caused cross-pollination. On examining the stigmas of young flowers under the microscope, I found that there were numerous, transparent, rounded protuberances over their surfaces. On examining mature stigmas, I found that there was a general enlargement of

the stigmatic surface, with the development of about a dozen of the protuberances into elongate, inverted, flask-shaped hairs, which contained a red fluid, and stood out above the colourless, rounded projections. These coloured outgrowths are probably the secretory hairs of the stigma.

The flower-clusters in most cases become red-tipped as they mature; even if they are not quite red, the style will be seen to become pink, and the corolla-lobes will have a pink streak here and there. I have seen many of these red clusters, in the latest period of their development, wet and shining with the overflowing nectar secreted by the surface of the ovary. Another interesting feature is, that the flower-clusters show a marked, initial zygomorphy of the inflorescence. Mr. John McLean Thompson, M.A., B.Sc., in a paper published in the Transactions of the Royal Society of Edinburgh (Vol. xlix., 6, 691), entitled, "Studies in Floral Zygomorphy," states that: "When any member of a cycle of floral parts shows a definite tendency to reach a developmental stage in advance of the remaining members, or to have the attainment of a developmental stage delayed, zygomorphy is initiated. The zygomorphy may be only temporary, in which case morphological actinomorphy may be restored."

The individual flowers of *D. fascicularis* exhibit initial, pistillate zygomorphy, and there is a marked initial zygomorphy of the inflorescence; for, in almost every cluster, there is a distinct zone of mature, or almost mature flowers, representing roughly one-half of each cluster, while the other half is in bud, or in various stages of early development. An examination of over ninety flower-clusters, on plants in various districts, showed that the flowers develop one after another, but that, about half-way in the development of the cluster, there is a distinct zone of almost mature, closed flowers; while, in the other half, the flowers are young or in bud. At this stage in the growth of the cluster, the flowers are usually all white, or the zone of maturer development is becoming pink. The individual flower, at its maturity, establishes morphological actinomorphy; and, later, the morphological actinomorphy of the inflorescence is attained.

This initial zygomorphy of flower and inflorescence is a distinct gain to the plant, for each cluster, at one period of its existence, will have flowers with elongated styles, carrying the mature stigmas ready to receive pollen; and other flowers, with shorter styles, with large pollen-masses ready for the visitor to carry them away; so that every visit to such clusters means an opportunity of both giving and receiving pollen at the one visit. The clusters are very often grouped closely, so that general cross-pollination is more easily effected. The introduced hive-bees are constant visitors to these flowers during the winter months. But they are useless guests, for they rarely touch the stigmas of the flowers; and only occasionally did I see them brush off the pollen with their wings. They approach the clusters from the side, usually, and walk between the groups of styles without touching the stigmas. They seem to visit the more mature clusters with closed flowers, and it was amusing to watch their efforts to get open the corolla-lobes in order to reach the nectar. Sometimes, in their efforts to force open the flowers, they seem to stand on their heads; and I have seen them force apart the mouth-parts in their endeavours to push the sucking-mouth through to the nectar.

In June and July, 1915, I observed, several times, honey-eaters of two species on these bushes. One species of honey-eater was very shy, and I could not identify it; but I saw the birds fly from flower to flower, and from one Darwinia bush to another. On another occasion, I observed a pair of the Spinebill Honeyeater (*Acanthorhynchus tenuirostris*) on one of the plants; and I was able to get within six feet of them, and watch, at leisure, their feasting on the flower-clusters. They approached mostly from the side, and sent their long bills into the flower-groups, their heads rubbing against the styles. They visited the white-coloured clusters, as well as the red ones. After a time, I stood up, but the birds just looked up, flew to another cluster, and went on feeding. It was only when I moved towards them that they flew off. Unfortunately I had not a camera. On that occasion, Miss Le Plastrier was with me, but she was observing another patch of Darwinia thirty yards away; she, too, saw birds of both species alight, and

visit the flower-clusters of *D. fascicularis*. The visitations of these birds, then, make the cross-pollination of *Darwinia* very simple, for the pollen-masses held by the substigmatic hairs, and carried up by the elongating style, are carried off by the bird as its head brushes the flowers. At the same time, pollen is placed on the stigmas of mature flowers, either of the same cluster or of adjacent ones. The closing of the corolla-lobes is a means of keeping out small creeping insects which would be useless to the flowers, because they might steal the nectar, without touching the stigma or the pollen below it.

These plants, when once established in a district, are plentiful, and must fruit freely.

I examined dozens of mature flower-clusters to see if there was any sign of the stigmas being brought down to meet the remains of the pollen-masses on the substigmatic hairs, and so causing self-pollination, should cross-pollination have failed to take place; but there was not one style which had so bent in order to bring the stigma in contact with the hairs.

I also noticed that it was only in comparatively few flower-clusters that there was an excessive supply of nectar so as to run over the edges of the flowers of such clusters; and I wondered whether, in these inflorescences, visitors had not come, and the excessive nectar was given off to make a special attraction (for such flowers glitter in the sun), or whether it was the result of the accumulation of unused nectar.

The pollen-grains of *D. fascicularis* are typical of the Natural Order Myrtaceæ, being formed of two curved, solid triangles, base to base, with clear triangular outlines, when viewed under the microscope. At each of the truncate angles of the pollen-grain, there is a button-like, transparent protuberance, which marks the spot where the pollen-tube may issue. I put some of the grains in a weak sugar-solution over night, and tubes had developed in the morning.

I submerged flowers in water, and found, after two days, dozens of pollen-grains with well-advanced germ-tubes developed. One interesting example was seen of a mass of pollen on the substig-

matic hairs with germ-tubes developed; and nearly all the tubes were stretched out towards the stigma, which was turned slightly downward, owing to the style having been fractured just below the stigma. These grains germinate very readily. After trying them half a dozen times, more than half the grains developed in one night, that is within twenty-four hours.

EXPLANATION OF PLATE LIX.

Pollination of *Darwinia fascicularis*.

- Fig. 1.—Inflorescence with actinomorphy restored.
Figs. 2-3.—Young flowers, showing the viscous pollen-mass.
Fig. 4.—Mature closed flower.
Fig. 5.—Flower viewed from above, with the viscous pollen-mass.
Fig. 6.—Stamen showing four pollen-sacs.
Fig. 7.—Mature stamen.
Fig. 8.—Pollen-grains, *b* and *c* with germ-tubes.
Fig. 9.—Stigma, and substigmatic hairs with pollen.
Fig. 10.—Mature stigma.
Fig. 11.—Fruits.

(All figures much enlarged.)